Morphological and Behavioral Adaptations to Desiccation in the Intertidal Limpet *Acmaea (Collisella) strigatella*

BY

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(7 Text figures)

INTRODUCTION

THE DISTRIBUTION OF INTERTIDAL organisms on rocky shores is determined by a number of factors, among which tolerance of desiccation is generally recognized to be of importance. The absolute tolerance to desiccation probably determines the upper limits of the vertical range for most intertidal species (CONNELL, 1970). Studies of adaptations to desiccation in the gastropod mollusks have involved two distinct approaches. The first approach has been experimental, where the investigators have compared the abilities of individuals from different areas of the vertical range to withstand desiccating conditions (BROEKHUYSEN, 1940; BROWN, 1960; DAVIES, 1969; WALLACE, 1972). The second approach has involved the analysis of shell shape and size in limpet gastropods that occur at different levels in the intertidal zone (RUSSELL, 1907; ORTON, 1933; MOORE, 1934; RAO & GANAPATI, 1971). In these studies limpets occurring at higher levels were observed to be structurally different from limpets at lower levels. The forms from higher levels displayed a tall, conical shell, while those from lower levels had a flattened, conical profile with an enlarged shell circumference. The significance of these differences in shell morphology appears to be related to the increased water-holding capacity that the limpets at higher levels possess. The only study to clearly show this relationship was conducted by SEGAL (1956a) on the limpet *Acmaea (Collisella) limatula* Carpenter, 1864, at Palos Verdes, California. For a given body weight the shells of limpets from higher levels were thicker and had a smaller total internal volume than did those from lower levels. However, the smaller shell volume reported for specimens from higher levels was more than compensated for by the smaller size of the soft parts of the animals. This resulted in a greater extra-visceral volume (and therefore a greater water-holding capacity) in the *A. limatula* from higher levels. The present study extends the comparative approach of SEGAL (1956a) by examining extra-visceral space in *A. (C.) strigatella* Carpenter, 1864 [1] collected from the upper and lower portions of its vertical range on a concrete seawall.

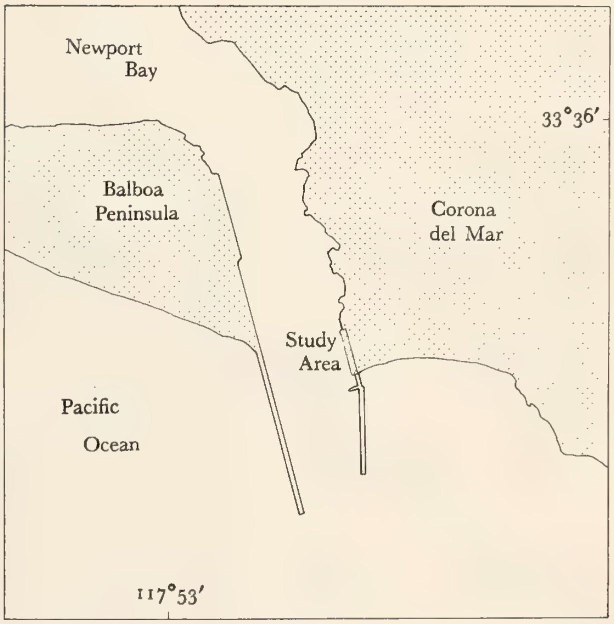

Figure 1

Location of Study Area in the Entrance Channel to Newport Bay, California, 33°35′36″ N Lat.; 117°52′38″ W Long.

[1] The taxonomic status of *Acmaea (Collisella) strigatella* was clarified recently by McLEAN (1969) who considered *A. paradigitalis* Fritchman, 1960 to be a synonym.

Behavioral responses to changes in desiccation stress by the limpet *Acmaea (Collisella) digitalis* Rathke, 1833 have been reported by FRANK (1965) and BREEN (1972). Both authors reported vertical migration by *A. digitalis* to higher levels in the intertidal zone during winter months. In the present study patterns of seasonal migration in *A. strigatella* are examined in relation to changes in desiccating influences.

METHODS

The study area (Figure 1) is located on the west-facing concrete seawall in the entrance channel to Newport Bay, Orange County, California. Specimens of *Acmaea strigatella* to be used for laboratory analysis were collected from a low-level sampling zone located between the tidal levels of +0.2 to +0.6 m (= +0.5 to +2 ft.) and from a

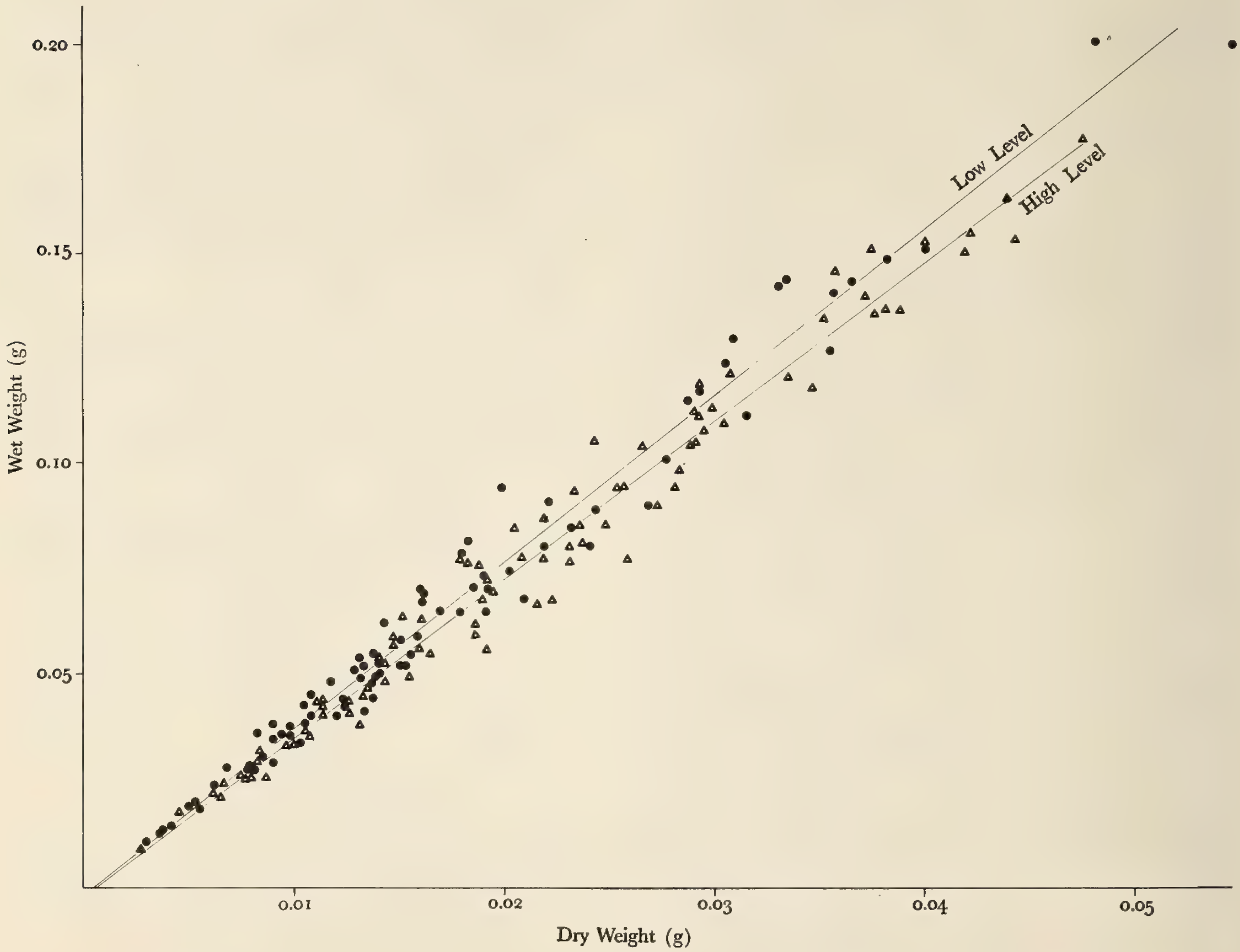

Figure 2

Relation between Fresh Wet Weight and Dry Weight in Specimens Collected in January and July 1971 from the High-Level (●, Y = −0.003 + 3.771 X) and Low-Level (▲, Y = −0.003 + 4.005 X) Sampling Zones high-level sampling zone situated between +1.5 to +2.0 m (=+4.5 to +6ft.), relative to 0 Datum at Mean Lower Low Water. Collections were made during November and December 1970 and January, February and July 1971. Positive identification of questionable specimens of *A. strigatella* was resolved by analysis of the radular ribbons, following the method of FRITCHMAN (1960).

Extra-visceral volume was obtained as the difference between shell volume and soft part volume by an approach similar to that of SEGAL (1956a), with modifications that permitted the accurate measurement of very small (0.02 to 0.40 cm^3) specimens. Each shell was mounted on a lump of soft wax with the shell apex pointing downward and the lowest point on the shell rim in the line of sight of a horizontally-oriented dissecting microscope. The shell was then filled with n-butanol from a micrometer syringe that was read to the nearest 0.001 ml. Normal butanol was used because of its low surface tension and vapor pressure. A statistical test to estimate required sample size (DIXON & MASSEY, 1969: 80) indicated that 7 or more measurements were sometimes necessary to estimate volume for the larger shells, while as few as 4 trials were often adequate for smaller shells.

The body volumes of the limpets were obtained indirectly by dividing wet weight by a density value of 1.038g per cm^3. The density value was experimentally determined from 13 volume displacement trials each performed with 8 limpets of known total weight (95% confidence limits = 1.038 ± 0.021 g/cm^3). Freshly collected limpets were weighed to the nearest 0.001g. Although a consistent blotting procedure was employed prior to making each wet-weight measurement, small variations in blotting efficiency apparently were responsible for large differences in resultant wet-weight values. To surmount this problem, 186 limpets were collected from the high- and low-level sampling zones during January and July 1971. These specimens were blotted and weighed, and were then oven dried at 85° C to constant weight (usually 48 hours) and reweighed. These data displayed linear regressions for individuals from high-level and low-level sampling zones (Figure 2). An F test for comparison of slopes indicated that the 2 regressions were significantly different ($P < 0.05$). The wet weight values for all limpets used in the calculation of body volumes were determined from dry weight measurements, using the regression equations calculated in Figure 2.

The vertical movements of *Acmaea strigatella* were followed during the months of May to August 1971. On April 30, 22 individuals located between +1.0 and +1.5 m were marked with enamel paint, and their positions were recorded with respect to small reference spots of paint on the substrate. The marked limpets were allowed 24 hours to seek preferred positions on the substrate. The position of each individual on 1 May 1971 was then taken as the starting point from which vertical displacement was recorded during the daylight hours at about 10-day intervals.

RESULTS

Extra-Visceral Space

Data obtained from samples collected in November and December 1970, in January and February 1971 and in July 1971 were used to construct graphs (Figures 3, 4,

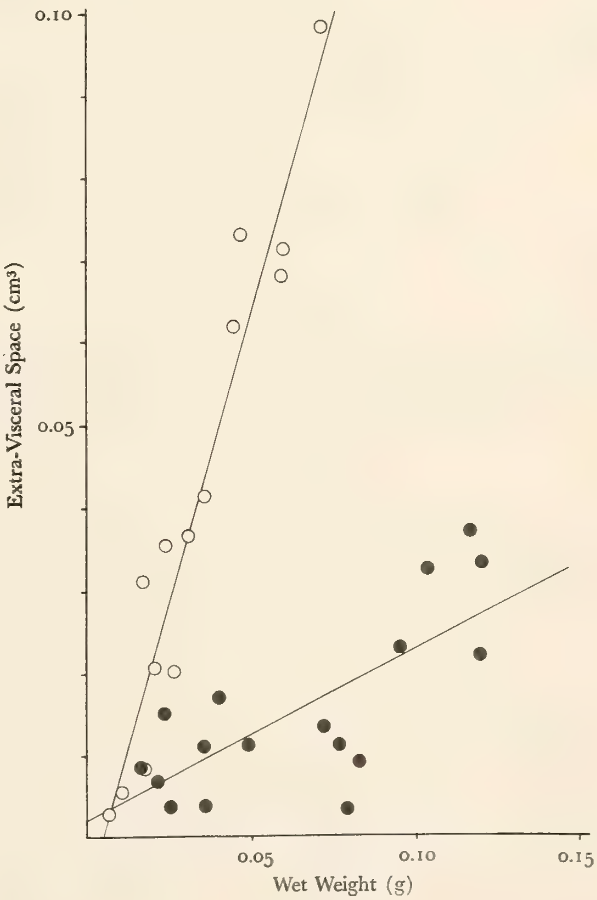

Figure 3

Relation between Wet Weight of Soft Parts and Size of the Extra-Visceral Space for Specimens from the High-Level (○, $Y = -0.008 + 0.693X$) and Low-Level (●, $Y = 0.002 + 0.104X$). Sampling Zones collected in November and December 1970.

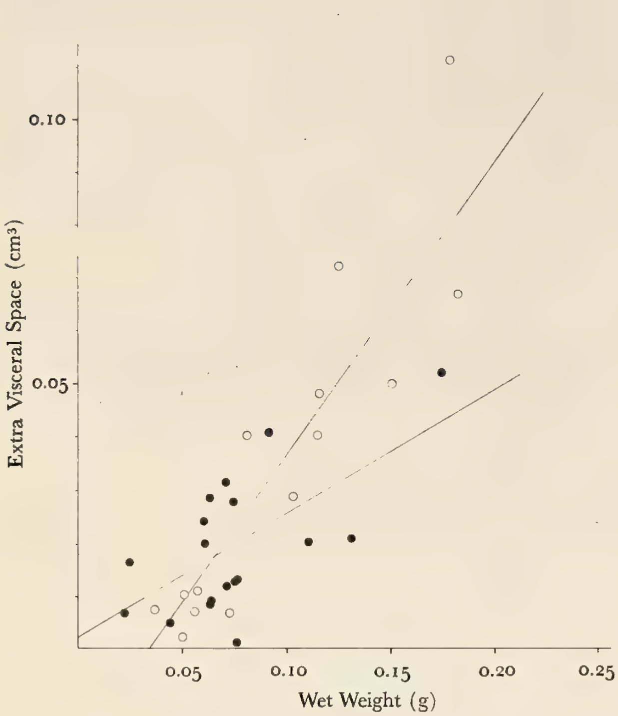

Figure 4

Relation between Wet Weight of Soft Parts and Size of the Extra-Visceral Space for Specimens from the High-Level (○, $Y = -0.019 + 0.560X$) and Low-Level (●, $Y = 0.004 + 0.235X$) Sampling Zones collected in January and February 1971.

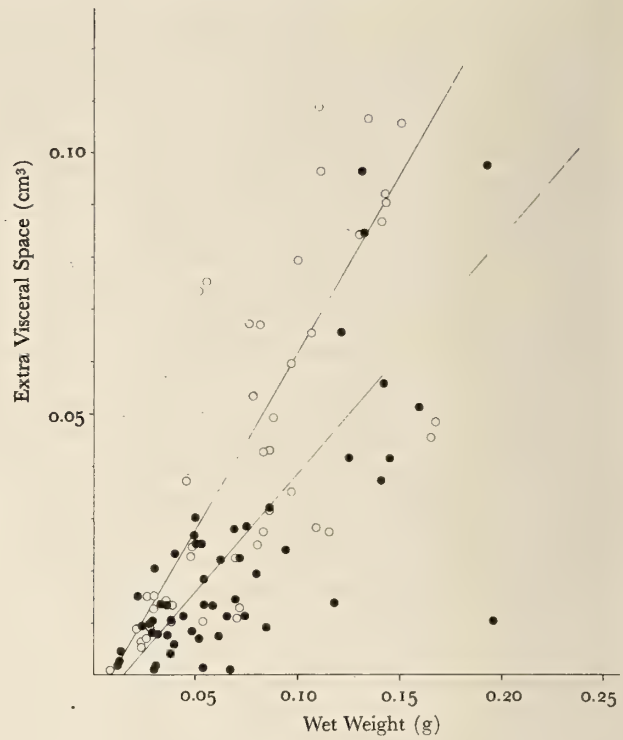

Figure 5

Relation between Wet Weight of Soft Parts and Size of the Extra-Visceral Space for Specimens from the High-Level (○, $Y = -0.006 + 0.689X$) and Low-Level (●, $Y = -0.006 + 0.457X$) Sampling Zones collected in July 1971.

and 5) relating the size of the extra-visceral space to the wet weight of limpets from the high- and low-level sampling zones. For each sampling period, the data from high- and low-level sampling zones were compared by analysis of covariance (Dixon & Massey, 1969). For November and December (Figure 3), F tests for comparison of variances and slopes revealed that high- and low-level samples differed significantly ($P < 0.001$). With the exception of small individuals, limpets of any given size (as measured by soft part weight) from the high-level sampling zone had larger extra-visceral spaces than did those from the low-level sampling zone. The regression lines in Figure 3 allow limpets of a given weight from each sample to be compared. For example, a high-level limpet weighing 0.030 g possesses an extra-visceral space of 0.037 cm^3 (corresponding to about 120% of its body volume), while the extra-visceral space of an 0.030 g low-level limpet is only 0.008 cm^3 (corresponding to only 27% of its body volume).

For the January-February 1971 sample (Figure 4) F tests indicated that the variances about the regression lines were not significantly different ($P > 0.05$), although the slopes were significantly different ($P < 0.005$). For the July 1971 sample (Figure 5), F tests indicated significantly different variances ($P < 0.05$) and slopes ($P < 0.005$). It is noteworthy that the slopes for the high-level samples in Figures 3 to 5 were reasonably consistent, while the slopes for the low-level samples were quite variable. These latter slope differences suggest the hypothesis of vertical migrational movements by limpets on a seasonal basis, with the strongest vertical separation of high- from low-level forms occurring at the time of the November-December sampling.

Migration

Qualitative observations were made on the vertical distribution of *Acmaea strigatella* at the study area during November 1970 to February 1971. Fewer limpets were observed in the high-level sampling zone (+1.5 to +2.0 m) during January and February than during the preceding 2 months. Limpets in the high-level zone were rarely observed above +1.6m during January-February. These observations suggest that high mortality or a downward migration, or both, had occurred during December and January. Mortality cannot be ruled out as a causal explanation for the reduction in numbers in the high-level sampling zone. However, a downward migration is also

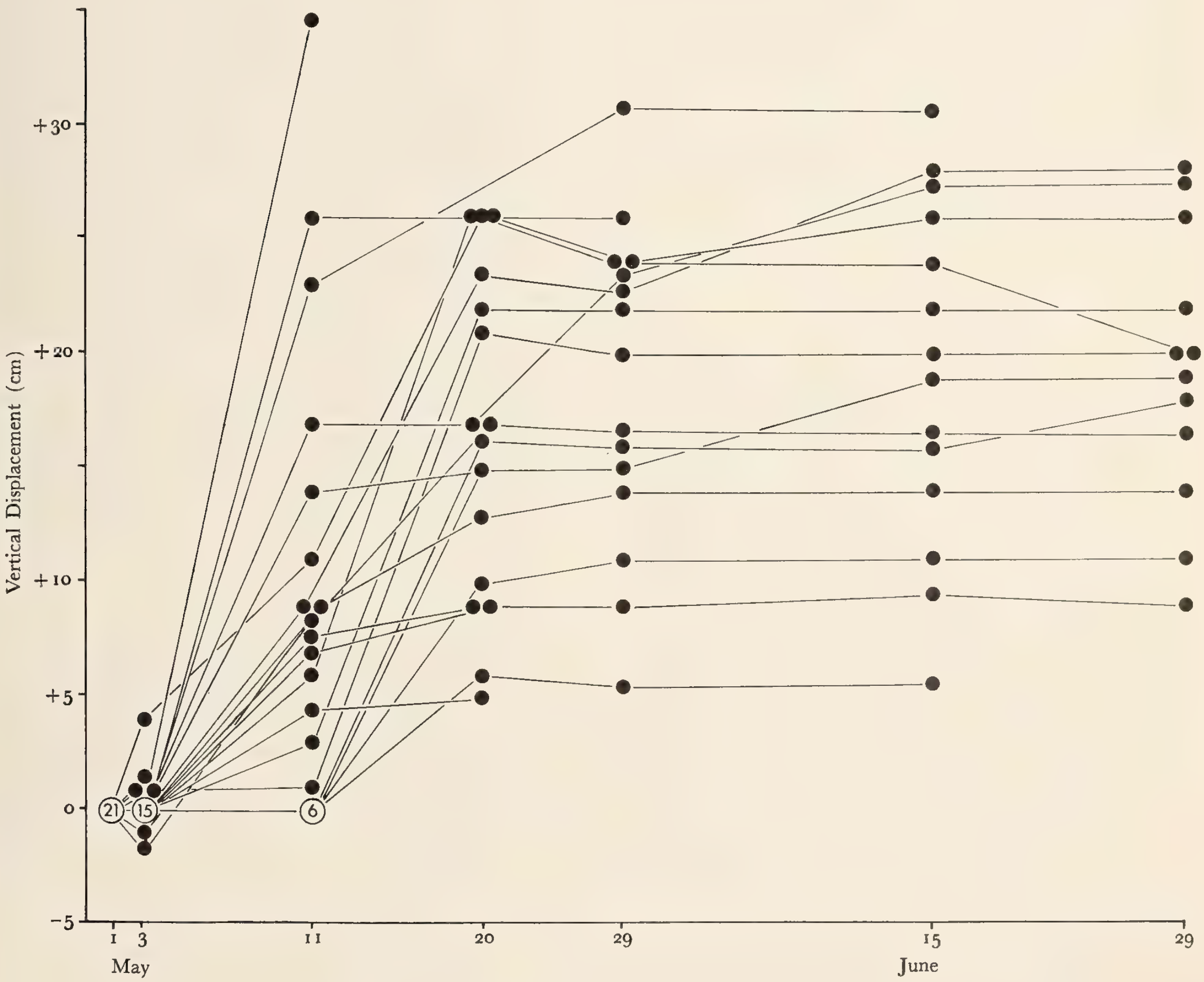

Figure 6

Vertical Movement of Marked Individuals as a Function of Time, Measured as Vertical Distance of Movement from Individual Starting Positions Established on 1 May 1971. The Vertical Movements of each Marked Limpet from one Date to the Next are indicated by Connecting Lines.

plausible, and could represent a behavioral response to increasing desiccation stress. A possible explanation of how desiccation stress could increase at this time of year will be presented in the discussion section.

During late April 1971 an observation was made that suggested the initiation of movement of limpets to higher levels. Several limpets were located at about +1.3 m bearing thalli of *Enteromorpha* sp. on their shells. At this time *Enteromorpha* sp. occurred only below +0.6 m. In order to follow the suspected upward migration of limpets after April, the movements of 22 marked individuals occurring between +1.0 and +1.5 m were recorded (Figure 6). The majority of individuals exhibited no net vertical displacement through May 3. By May 20, however, it was apparent that a dramatic upward migration had occurred. The mean upward displacement between May 1 and May 20 was 17.2 cm. The positions of marked limpets from May 20 to June 29 were remarkably stable. When the study area was visited in mid-July, insufficient numbers of marked individuals could be located, and monitoring was discontinued.

DISCUSSION

The comparative measurements of extra-visceral space for *Acmaea strigatella* from high- and low-level sampling zones during November and December 1970 (Figure 3) are in agreement with the results of SEGAL's (1956a) study on *A. limatula*. Both species possess a broad vertical range in the intertidal zone and distinct morphological differences within this vertical range were recorded. Reproductive and physiological differences within a limpet's vertical range would also be predicted, and have been reported for *A. limatula* by SEGAL (1956b) and SEGAL & DEHNEL (1962), and for *A. (Collisella) scabra* (Gould, 1846) by SUTHERLAND (1970). In the present study the comparison of wet to dry weight of limpet soft parts (Figure 2) suggests vertical differences in the osmotic state of the body fluid. *Acmaea strigatella* occurring at higher levels had wet weights that averaged 6% less than wet weights of individuals at lower levels having the same dry weight.

Seasonal differences in samples collected from the low-level sampling zone were suggested by the data of Figures 3, 4, and 5, and may be interpreted in relation to hypothetical vertical migratory movements. The slope for the low-level regression line was steeper for the January-February sample ($b = 0.235$) than for the November-December sample ($b = 0.104$). This change in slope could be explained by a downward migration during December and January, resulting in the introduction of limpets from higher levels into the low-level sampling zone.

Vertical migrational movements during the winter have been reported for *Acmaea digitalis* by FRANK (1965) at Coos Bay, Oregon and by BREEN (1972) at Port Renfrew, British Columbia. Instead of migrating downward during the winter, as suggested here for *A. strigatella, A. digitalis* migrated upward. This upward movement occurred at a time when increased wetting of the high intertidal zone took place as a consequence of increased wave splash. Lowered air temperatures and coastal fog during the winter months also favor extended periods of tidal exposure. Breen considered the occurrence of higher high tides during the day time and lower low tides between dusk and midnight in British Columbia to favor migration to higher levels. An explanation for the difference in direction of migration in the present study would appear to lie in the nature of the study site at Corona del Mar, rather than in the species concerned. The site (Figure 1) is unique in that it is protected from heavy surf (except when swells approach from the south) and the rocks and concrete wall from which the limpets were collected face 15° south of due west. This situation makes these limpets particularly susceptible to afternoon insolation. The time of day at which the lowest tides occur (and hence the longest periods of exposure to air) varies from month to month. Afternoon lower low tides are much more frequent in the winter than at other times (Table 1). The frequency of afternoon tidal exposure began to increase greatly during November and reached a peak in January and February. This phenomenon and the fact that the study site receives direct exposure to the sun in the after-

Table 1

Number of Days per Month When Minus Tides (Tidal Levels below 0.0 Datum) occurred during the Afternoon

Month	Number of Days
July (1970)	0
August	0
September	0
October	7
November	12
December	13
January (1971)	15
February	16
March	11
April	4
May	0
June	0

noon could account for the downward migration suggested to have taken place in January 1971.

During the month of May a mean upward movement of 17.2 cm was recorded (Figure 6). This upward migration may have been an anomalous situation for this time of year, because movement was possibly triggered by a stormy, overcast period observed during the first 2 weeks of May. Greatly increased wave splash was observed at this time.

The migration of *Acmaea strigatella* to lower levels during the summer months would have had to occur in early July in order to explain the data on extra-visceral space for the low-level sampling zone during the latter half of that month (Figure 5). Explanation of a slope of 0.457 for the low-level sampling zone requires the downward movement of limpets from higher levels. That such a downward migration could have occurred during early July is partially supported by the tidal pattern for this period of time (Figure 7). Four dates were selected here to illustrate the progressive occurrence of higher high tides at later times during the afternoon, accompanied by exposure of the intertidal region above about +1.2 m (= +4 ft.) during the preceding daylight hours. Plotted separately beneath the tidal curves for each date are records of air temperature and wind velocity taken at 3-hour intervals between 0400 and 1600 hrs (Orange County Harbor District records for Newport Bay, taken at a weather station located approximately 0.8 km north-northeast of the study site). Air temperature did not appear to be limiting by itself, as the maximum temperature attained during the first 10 days in July was only 23° C. Averaging the air temperature data over the 10-day period (Table 2), a stable pattern emerges of mild early morning temperatures (about 17° C at 0400 hrs) which rose only slowly during the day to about 21° C at 1600 hrs. An examination of data on wind velocity, however, suggests considerable variability between the 4 dates selected in Figure 7. This variability is also evident for the averaged

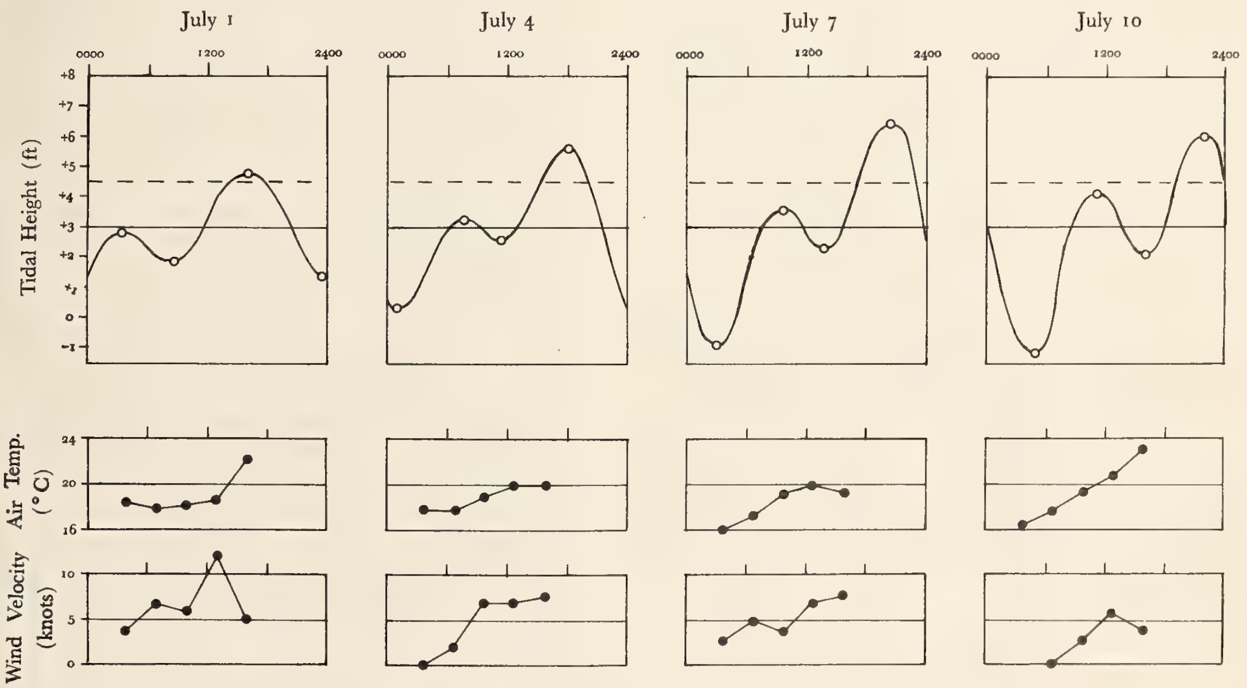

Figure 7

Tidal Curves for 1, 4, 7, and 10 July 1971 (constructed from tidal data for Los Angeles Harbor, 1971 Tide Tables, U. S. Department of Commerce, Air Temperatures and Wind Velocities at 3-hour Intervals (between 0400 and 1600 hrs) at Newport Harbor are included for each Date (see text for location of weather station).

Table 2

Averaged Air Temperatures and Wind Velocities at 3-hour Intervals between 0400 and 1600 hrs for 1 - 10 July 1971

	Time of Day (hrs)				
	0400	0700	1000	1300	1600
Averaged Air Temperature in °C [1]					
	16.95	17.40	18.94	19.77	20.94
	(0.66)	(0.57)	(0.80)	(1.08)	(1.14)
Averaged Wind Velocity in Knots [1]					
	2.20	2.50	4.50	8.10	6.60
	(2.56)	(2.41)	(2.06)	(2.26)	(1.62)

[1] N=10, ( ) denotes one standard deviation

data over the 10-day period (Table 2). High standard deviations were recorded for each mean value and a maximal daily wind velocity of 6 to 10 knots occurred at 1300 hrs. A consistent feature of the 10-day period was the occurrence of southerly winds at 0400 hrs and progressive rotation of wind direction from the south to southwest by 1600 hrs. Thus, the morning and early afternoon exposure by the tides, coupled with warm air temperatures and a southerly to southwesterly breeze of up to 10 - 12 knots (in the afternoon) could have created sufficient desiccation stress in higher-level *A. strigatella* to induce the hypothesized downward movements. At some time during the fall months of 1971, limpets originally from higher levels would have had to migrate upward from the low-level sampling zone, if the November-December sample of 1970 is to be considered predictive for other years.

In the preceding discussion, we have made the assumption that vertical movements by *Acmaea strigatella* above about +1 m are affecting the specific composition of the low-level sampling zone in terms of extra-visceral space. Although the assumption would appear reasonable, it must be qualified since data on vertical movement below +1 m were not obtained.

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